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BIODIVERSITY RESEARCH

Predicting the subspecific identity of invasive species using distribution models: *Acacia saligna* as an example

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ABSTRACT

Aim To explore whether the subspecific genetic entities of *Acacia saligna* occupy different bioclimatic niches in their native and introduced ranges and whether these niches are predictable using species distribution models (SDMs).

Location Australia, South Africa and the Mediterranean Basin.

Methods Species distribution models were developed in MAXENT using six climatic variables to calculate the climatic suitability of the ranges of *A. saligna*. We assessed (1) the subspecific niche differences identified by SDMs using measures of niche overlap and model performance; (2) the ability of SDMs to predict the most likely subspecific genetic entities present in South Africa based on comparisons to genetic data; and (3) the ability of SDMs to predict the most likely subspecific genetic entities present in the Mediterranean Basin. All model projections were assessed for sensitivity and modelled prevalence as indicators of model fit and predictability.

Results The SDMs identified different subspecific bioclimatic niches in the native range. Sensitivity and modelled prevalence show that none of the models correctly predicted the full range of *A. saligna* in South Africa or the Mediterranean Basin. Models also show that the South African niche is different to that in the native range.

Main conclusions Subspecies of *A. saligna* occupy quantifiably distinct bioclimatic niches in their native ranges, implying that they should occupy distinct niches in their invasive ranges. However, projections to the introduced range did not correspond with known occurrences. Our SDMs are unable to predict the full introduced niche of *A. saligna* at a species or subspecies level in either South Africa or the Mediterranean Basin. Range limits in the native and introduced ranges may be determined by additional factors not used in the SDMs developed in this study.

Keywords
Acacia saligna, **biological invasions, correlative models, invasive species, niche conservatism, species distribution modelling, subspecies.**

INTRODUCTION

Human activities are changing the geographical ranges of species in many ways at faster rates and at broader scales than ever before (Vitousek *et al.*, 1997; Walther *et al.*, 2009). Many types of changes to the environment caused by anthropogenic factors affect the capacity of organisms to persist at a given locality. Such changes, together with a reshuffling of associated biotic interactions, have radically altered the distribution of species worldwide. Rapidly growing human populations with increasing mobility, diversified needs and technological advances have created new pathways for the movement of species to areas far removed from their native ranges (Wilson *et al.*, 2009). A proportion of introduced species become

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invasive (i.e. spread from introduction sites), in some cases displacing native species, altering ecosystem functioning and causing environmental and economic damage (Pyšek & Richardson, 2010).

Species distributions are constrained by biotic and abiotic factors that define the space or the 'niche' that a species can occupy (Elith & Leathwick, 2009; Alexander & Edwards, 2010). Species distribution models (SDMs), also termed bioclimatic models or ecological niche models, are used to understand the distribution of species (Elith & Leathwick, 2009). They attempt to incorporate a number of meaningful biological and environmental factors that influence a species' range. For invasive plant species, there is often a marked similarity between the climate in the native range and other areas where the species is most invasive (Thuiller *et al.*, 2005). Consequently, climate matching between the native and introduced range of a species using SDMs is widely used to forecast future invasion risks (Tucker & Richardson, 1995; Peterson *et al.*, 2003; Mau-Crimmins *et al.*, 2006; Richardson & Thuiller, 2007; Gordon *et al.*, 2010).

Most SDMs assume the subject taxon (usually a species) comprises a uniform entity; that is, the subject taxon has similar environmental adaptations throughout its range. This is rarely the case. SDMs also assume that a species' niche is conserved between the native and introduced range (niche conservatism *sensu* Peterson *et al.*, 1999). However, realized niches (the niche actually occupied by a species) are unlikely to be the same once an invader is released from its natural enemies and competitors in the introduced range (Lee, 2002) or if genetic drift occurs. Genetic drift may result in the introduced species being represented by only a small part of the total genetic diversity present in the native range (i.e. a genetic bottleneck; Mooney & Cleland, 2001).

The amount and structure of genetic diversity in the introduced range will likely affect a species' ability to withstand competition or environmental pressures in its new range. Any positive effects, such as faster growth rates or resistance to herbivory, may allow an introduced species to expand its range or move beyond its native realized niche. Whether the differences between a species' native and introduced genetic structure will consistently enable an invader to alter its niche (lack of niche conservatism; see Peterson *et al.*, 1999; Wiens & Graham, 2005) is currently unknown (Rödder & Lötters, 2009).

Previous research has shown that the genetic structure of a species interacts with aspects of the introduction history to determine the genetic diversity and structure in the introduced range (e.g. Le Roux *et al.*, 2011). Several studies have reported admixture (mating between two genetically distinct groups) resulting in highly invasive novel genotypes as a consequence of multiple introductions from a highly structured and diverse native range (Gaskin & Schaal, 2002; Genton *et al.*, 2005; Lavergne & Molofsky, 2007; Facon *et al.*, 2008; Prentis *et al.*, 2008).

The capacity of SDMs to accurately project potential distributions may be substantially affected by a number of parameters including whether subspecific entities have adapted to different climatic niches; whether the processes defining niches differ in the introduced and native ranges or whether an invader undergoes substantial genetic change upon introduction. Given the significant implications for obtaining meaningful output from SDMs, it is surprising that very few studies have tested or incorporated known subspecific information into SDMs, even for conservation-focused models of native species (see Scoble & Lowe, 2010). A small number of studies have used molecular data and SDMs to delimit the range of a number of closely related species (Leaché *et al.*, 2009); assess changes in a species' spatial genetic structure with climate change (Sork *et al.*, 2010); assess the change in niche occupancy of sister species with change in climate (Pearman *et al.*, 2010); and assess the biogeographical history of two congeneric species (Jakob *et al.*, 2007) and possible speciation mechanisms (Graham *et al.*, 2004; Peterson & Nyári, 2007). However, to our knowledge, SDMs have not been developed at a subspecies level for an invasive alien plant.

Australian acacias (species in *Acacia* subgenus *Phyllodineae* native to Australia; Miller *et al.*, 2011; Richardson *et al.*, 2011) are an excellent system for exploring these ideas as many invasive acacias have geographically structured intraspecific variation in their native range (Broadhurst *et al.*, 2001; Byrne *et al.*, 2002) and have different introduction histories (see Le Roux *et al.*, 2011). We test the potential for using subspecific information on the *Acacia saligna* (Labill.) H.L. Wendl. species complex. *Acacia saligna* is native to Western Australia and has been widely introduced around the world, becoming an aggressive invader in many regions (Henderson, 2001; Nel *et al.*, 2004; Richardson & Rejmánek, 2011). It has been well studied from both an ecological and molecular perspective in its native (Marsudi *et al.*, 1999; Maslin & McDonald, 2004; George *et al.*, 2006; Millar *et al.*, 2008, 2011) and introduced ranges (Milton & Hall, 1981; Witkowski, 1991; Holmes & Cowling, 1997; Sauerhaft, 1997; Wood & Morris, 2007; Yelenik *et al.*, 2007; Le Roux *et al.*, 2011), providing a substantial source of verifiable distribution records from which a SDM can be built.

Previous genetic research has shown that a number of subspecific entities of *A. saligna* exist in Western Australia (George *et al.*, 2006; Millar *et al.*, 2008), but their 'morphological taxonomic classification is problematic' (Millar *et al.*, 2011) making field identification challenging. Millar *et al.* (2008) identified four genetic lineages or subspecies, consistent with the morphological groupings of the species complex (Maslin *et al.*, 2006), each geographically associated with a particular ecological habitat: subspecies *lindleyi* (watercourses, sand dunes, coastal plains), subspecies *pruinescens* (deep soil in swamp-like areas), subspecies *saligna* (coastal plains) and subspecies *stolonifera* (watercourses and forest-like areas). More recently, following extensive population genetic characterization in the native range, the *A. saligna* species complex has been revised to comprise only three lineages. Millar *et al.* (2011) identified these three groups as: (1) subspecies *lindleyi*, (2) subspecies *stolonifera* and (3) subspecies *saligna* and *pruinescens*. For simplicity throughout this manuscript, we use the term subspecies to refer both to the original four taxa

based on morphological traits (Maslin *et al.*, 2006) and the more recent three taxa, derived from molecular research (Millar *et al.*, 2011), but recognize that neither scheme has been formalized.

Acacia saligna was introduced to South Africa on at least five separate occasions between 1845 and 1922, with over 200 million seeds introduced during this period (Poynton, 2009). A comparative phylogeographic study of native and introduced *A. saligna* populations showed that only a very small proportion of *A. saligna*'s native genetic diversity is present in South Africa (Le Roux *et al.*, 2011). This is despite the fact that introductions into South Africa were from multiple sources, including the native range in Australia, France and other unknown sources (Poynton, 2009). The species has a long residence time (*c.* 170 years) in South Africa and has been very widely dispersed. It has likely reached its bioclimatic limits at the broad scale in the region (Rouget *et al.*, 2004).

This study draws on available ecological and genetic research on the *A. saligna* species complex to: (1) assess whether the different subspecies occupy areas in their native range that can be distinguished by correlative SDMs; (2) explore the predictive ability of subspecific SDMs for the introduced range in South Africa considering known occurrences and current genetic data (Le Roux *et al.*, 2011); and (3) use SDMs to predict which subspecies are present in other biogeographical regions where *A. saligna* has been introduced (i.e. in the Mediterranean Basin).

METHODS

Modelling approach

Our approach incorporated the most recent recommendations and approaches in the literature associated with correlative modelling of introduced species (see Webber *et al.*, 2011), with each modelling approach tailored to the ecological questions being asked. Two data source regions were used to calibrate models representing the native range (Western Australia, Fig. 1a) and an introduced range (South Africa, Fig. 1b) of *A. saligna*. While native and introduced records are often combined in the same model to improve projections of the potential invasive range (e.g. Broennimann & Guisan, 2008), this would obscure any pattern attributable to the species' subspecific bioclimatic distribution, and we therefore chose not to use this approach.

To determine whether SDMs can detect subspecific niche differences (aim 1), we first built models using all native records to test the predictability of the full native niche of the *A. saligna* species complex. Second, we built models using native records per subspecies to test the predictability of the niche for each subspecies. In both cases, models were projected to the model training domain in the south-western part of Western Australia. We then used several methods to compare the identified climatic niches occupied by the subspecies.

To explore the predictive power of SDMs in the introduced range in South Africa, relative to known occurrences and genetic data, (aim 2), we used several approaches. First, models were built using all native records and projected to South Africa to assess the niche that the entire *A. saligna* species complex would occupy in the introduced range. Second, models were built using records per subspecies and projected to South Africa to assess subspecific niche differences in the introduced range. Third, models were built using various combinations of subspecies records and projected to South Africa. These combinations were selected to incorporate the most recent molecular groupings within the species complex (Millar *et al.*, 2011), and molecular evidence (Le Roux *et al.*, 2011) suggesting only a small proportion of the native genetic diversity is present in South Africa. The combinations tested were (*lindleyi* + *stolonifera; pruinescens* + *saligna; lindleyi* + *pruinescens* + *saligna; pruinescens* + *saligna* + *stolonifera*). Fourth, models were built using all introduced South African records and projected to the whole of South Africa. Fifth, models were built using records from the introduced range in South Africa and projected back to the native range in Western Australia. The fifth component compares the native and introduced niche within the same environmental space, allowing for any changes in the occupied range between countries to be assessed.

To determine whether SDMs can predict subspecies present in other biogeographical regions where *A. saligna* has been introduced (aim 3), we followed three approaches. Each approach projected to an area with a mediterranean-type climate similar to that in the south-western parts of Western Australia. For this aim, projections to the Mediterranean Basin enabled us to further explore the practicality of predicting subspecific identities of introduced *A. saligna* populations. First, models were built using all native records to assess the niche occupied by the entire *A. saligna* species complex. Second, models were built using native records per subspecies to assess subspecific niche differences. Third, models were built using South African *A. saligna* records to assess whether the invasive type present in South Africa is conserved in the Mediterranean Basin.

Distribution records

Native distribution records for each subspecies of *A. saligna* in Western Australia were obtained from herbarium records from Australia's Virtual Herbarium online database (http://avh.rbg.vic.gov.au, accessed 1 October 2010). We only considered records that were assigned morphologically to one of the four subspecies groups by the taxonomic authority on *A. saligna* (Bruce Maslin, Department of Environment and Conservation, Western Australia). Records that appeared to be outliers (i.e. located on the periphery of the known distributions of each subspecies) were verified by Bruce Maslin using the original specimen sheets. To ensure that presence records only reflected the natural climate suitability at a site, we omitted records that (1) were identified as cultivated or growing in managed environments, (2) occurred in microclimates not detectable at a 5′ grid scale (e.g. along rivers in arid areas) or (3) had locality

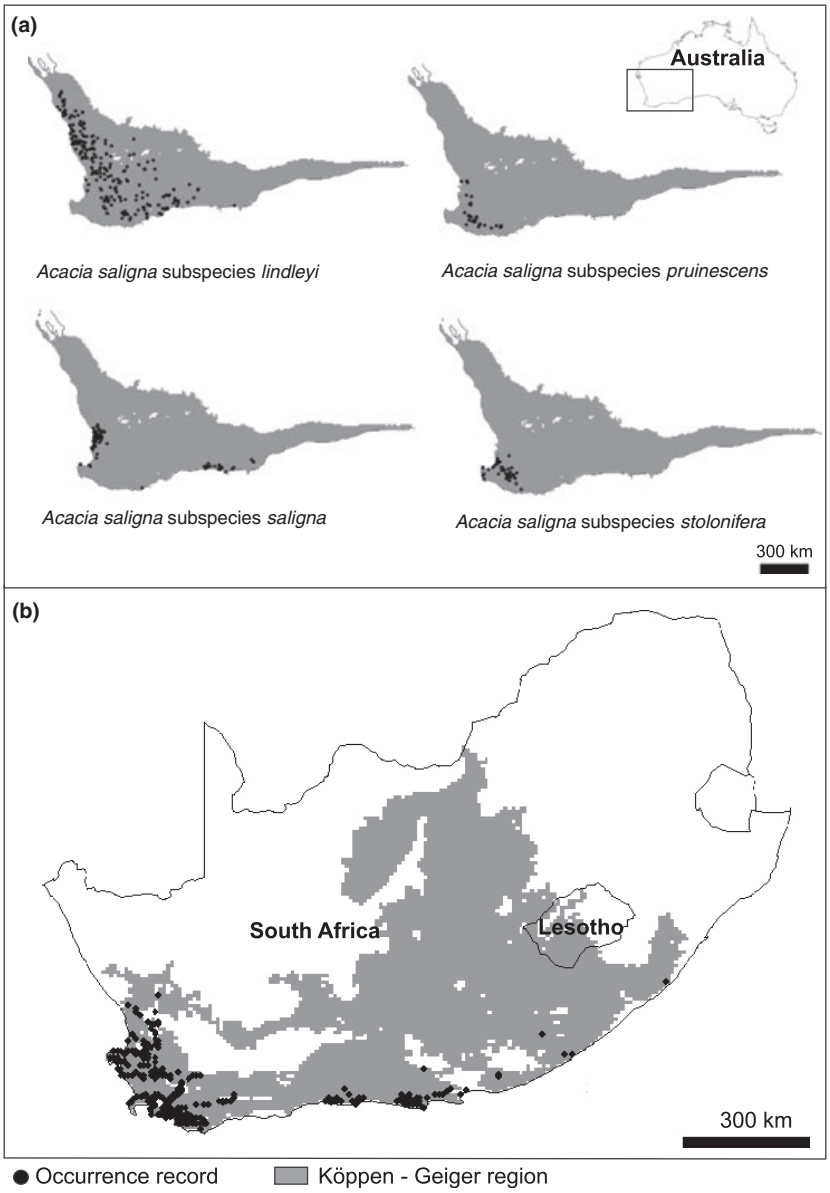

Figure 1 Distribution records (black circles) of *Acacia saligna* overlaid with an environmentally informative background (Köppen–Geiger region; grey shading) from which pseudo-absence data were drawn for (a) the four proposed subspecies in the native range in Western Australia and (b) the introduced range in South Africa and Lesotho.

information at a resolution coarser than 5′. After quality control, and restricting records to one per 5′ grid cell per subspecies (i.e. regularization to minimize sampling bias), a total of 442 occurrence records were used: 249 records for subspecies *lindleyi*, 44 records for subspecies *pruinescens*, 108 records for subspecies *saligna* and 41 records for subspecies *stolonifera* (Fig. 1a).

Distribution records for the introduced range in South Africa were compiled from the South African Plant Invaders Atlas (SAPIA; Richardson *et al.*, 2005; Henderson, 2007), as well as field observations and collections by the authors. These records were collected at a spatial precision of at least 5′ and subjected to the same quality control methods as the native range records. A total of 210 regularized occurrence records were used (Fig. 1b). These records contain no information on subspecific identity.

Distribution records for the introduced range in eastern Australia and the Mediterranean Basin were sourced from Australia's Virtual Herbarium online database and the Global Biodiversity Information Facility (GBIF, 2010), respectively. These records were subjected to the same degree of scrutiny as those records used to build the models. Only occurrences collected at a spatial precision of a 5′ grid cell were used. A total of 24 regularized occurrence records were used. These records contain no information on subspecific identity.

Bioclimatic variables

We wanted to build the models using bioclimatic variables that represent ecologically relevant climatic factors for *Acacia* distributions in mediterranean-type environments (Jeffery *et al.*, 1988; Witkowski, 1991; Degen *et al.*, 1995; Droppelmann

& Berliner, 2000; Maslin *et al.*, 2006). During variable selection, we placed a priority on choosing a set of variables that minimize multicollinearity between variables. Multicollinearity was assessed using a Pearson correlation coefficient analysis (see Table S1 in Supporting Information) using ENMTools version 1.0 (Warren *et al.*, 2010). We downloaded global gridded bioclimatic data at 5′ resolution from the WorldClim database (http://www.worldclim.org; Hijmans *et al.*, 2005) for the six selected bioclimatic ('BioClim') variables: temperature seasonality (Bio4), mean temperature of the hottest quarter (Bio10), mean temperature of the coldest quarter (Bio11), precipitation seasonality (Bio15), precipitation of the hottest quarter (Bio18) and precipitation of the coldest quarter (Bio19).

Species distribution modelling

MaxEnt version 3.3.3e (Phillips *et al.*, 2006) was used throughout as it is a widely used and accepted SDM method that can produce robust results (Elith *et al.*, 2006; Phillips & Dudík, 2008; Elith *et al.*, 2011). The software builds a model using environmental layers, occurrence records (presence points) and a geographically defined background area for taking pseudo-absence points for a particular species to define a set of constraints under which that species is likely to persist. We applied default parameters: 'logistic output', 'create response curves', 'jacknife measures of variable importance', 'do clamping' and a regularization value of 1. We restricted the feature type to 'hinge features'; selecting only hinge features means that the MaxEnt model produces smoother response curves where the models are more focussed on the 'strongest trends' in the data (Elith *et al.*, 2010) (see Fig. S1 and S2). This approach is recommended for introduced species and produces models that are likely to be more ecologically realistic (e.g. Elith *et al.*, 2010).

MaxEnt uses pseudo-absence data drawn randomly from a geographically defined background in lieu of actual absence records to define environmental conditions for where the species has not been recorded. The background from which pseudo-absences are drawn can however significantly influence the model results (Phillips *et al.*, 2009; VanDerWal *et al.*, 2009), and so it is recommended that the background be restricted to the region in which the species would reasonably be expected to occur (Elith *et al.*, 2011). Moreover, it is necessary to achieve a balance between a background that gives good regional performance driven by relevant climate variables and one that can perform reasonably at a continental scale by not being overly constrained by a reduced set of variables largely unrelated to the species in question (Elith *et al.*, 2010; Webber *et al.*, 2011). Following the methods of Webber *et al.* (2011), we used the Köppen–Geiger climate classification (or vegetation classes) to define our model backgrounds. Köppen–Geiger classifications, following the rules defined in Kriticos *et al.* (2011), were applied to the 5′ resolution WorldClim global climatology, which is the same source for the BioClim variables used in the models. Ten thousand pseudo-absences (Phillips & Dudík, 2008) were then drawn from an area defined by the Köppen–Geiger polygons within which one or more distribution records were located. For models based on native range subspecies records, we used a single background that corresponded to the combined distribution records of *A. saligna*. For all other models, we used the rules outlined above to define a background based on the distribution records used in that model.

Model projections to new areas, particularly to other continents, are likely to include regions where the model is extrapolating beyond the climate space encompassed by the training domain (i.e. the background). Thus, it is imperative that novel areas should be identified in projections so that the model output in these regions can be carefully interpreted against the response curves and assessed for plausibility (Elith *et al.*, 2010). Projections to novel climates (model extrapolation) were assessed using multivariate environmental similarity surface (MESS) maps (Elith *et al.*, 2010). MESS maps provide an indication of the similarity of the bioclimatic data in the projected region compared with the training region. Areas of dissimilar bioclimatic data (novel environments) are given negative values (MESS−, extrapolation), while areas of similar bioclimatic data are given positive values (MESS+, interpolation). MESS− areas were carefully interpreted by visually inspecting the response curves (Fig. S2) and limiting bioclimatic variables (Fig. S3) to provide an indication of the variables driving the models in different regions. We used the minimum training presence or lowest presence threshold (LPT; Pearson *et al.*, 2007) to define climatically suitable areas. The LPT is the lowest generated suitability value from model projections that intersects with a distribution record and therefore represents a non-arbitrary threshold particularly suited for modelling invasive species (Liu *et al.*, 2005; Webber *et al.*, 2011). Colour raster displays were separated into 20 classes ranging from the LPT value (green) to moderately suitable (yellow, probability value of 0.5) and highly suitable (red, probability value of 1). All values below the LPT were designated unsuitable (white).

Niche differences

To test whether the climatic niches derived from the four subspecies differed, we conducted niche similarity tests using ENMTools version 1.0 (Warren *et al.*, 2010) in the native range of *A. saligna*. ENMTools calculates Schoener's (1968) D index and the Hellinger-based similarity statistic (I) (Van der Vaart, 1998) for each grid cell of the model projection. This approach, suggested by Warren *et al.* (2008), provides an ecologically meaningful measure (D) that is combined with a statistically robust measure (I). In ENMTools, both measures range from 0 (no overlap) to 1 (complete overlap).

Model assessment

Correlative model fits were calculated by assessing how often the model correctly assigned presence or absence, based on actual presences and pseudo-absences. We used the LPT to

define 'presence' or 'absence' and based calculations on 5′ grid cells using regularized distribution record data. We calculated (1) model sensitivity, which is the proportion of correctly predicted observed presences (omission errors), and its statistical significance using an exact one-tailed binomial test (following the methods of Anderson *et al.*, 2002); (2) modelled prevalence, which is the proportion of the complete projection region estimated to be climatically suitable (for more details, see Webber *et al.*, 2011). In all cases, we assessed modelled prevalence in relation to model sensitivity, novel regions and extrapolation within these regions by examining the response of the bioclimatic variables in the model (response curves, Fig. S2).

Models that display high sensitivity (as close to 1 as possible) and are statistically significant (according to the exact one-tailed binomial test) are important for invasive species as they are at least able to correctly project occurrences in the introduced range. Models that display low sensitivity suggest models that are unable to project climatic suitability in regions where there are known occurrences. Further, models that display statistically non-significant outputs do not warrant further investigations as projections are unlikely to be robust. We did not use a commonly applied method (area under curve values of the receiver operating characteristic) to measure model performance because its usefulness for model interpretation is questionable (Lobo *et al.*, 2008), particularly when assessing models developed for invasive species (Webber *et al.*, 2011).

RESULTS

Models projected to the native range

Niche similarity tests (Schroener's D index and Hellinger-based distance) based on the projected climatic suitability for each subspecies indicated that the subspecies occupy different bioclimatic niches in their native range with respect to the six variables used in our models (Table 1). In addition, niche overlap for subspecies projections indicate that subspecies *lindleyi* and *pruinescens* have the most similar niches, while subspecies *lindleyi* and *saligna* have the most dissimilar niches (Table 1). These differences were mirrored by variation in the sensitivity and modelled prevalence for models calibrated using records for each subspecies (Table 2, aim 1).

All models trained and tested with native range occurrences displayed statistically significant results according to the exact binomial test ($P < 0.0001$, Table 2). Highly sensitive (Table 2) subspecies level projections to the native range (Fig. 2) indicate that the four subspecies of *A. saligna* occupy different climatic niches. Further, results showed that the climatic niche occupied by the species complex as a whole is broader than the niche occupied by each subspecies (Fig. 2a versus Fig. 2b–e). The projections for *A. saligna* subspecies *pruinescens*, *saligna* and *stolonifera* were subsets of the broad projected region of climatic suitability for *A. saligna* subspecies *lindleyi* (Table 1 and Fig. 2).

Table 1 Variation in the bioclimatic niche similarity of the subspecies of *Acacia saligna* in Western Australia. Pairwise similarities were calculated based on model (10 replicates) projections to the native range. Two measures describe the climatic similarity: niche overlap using Schoener's D index and niche similarity using the Hellinger-based similarity statistic. Both measures range from 0 (no overlap/similarity) to 1 (complete overlap/similarity).

Acacia saligna subspecies	Schoener's index (D)	Hellinger similarity statistic (I)
lindleyi – stolonifera	0.381	0.620
pruinescens – stolonifera	0.487	0.531
lindleyi – saligna	0.295	0.552
pruinescens – saligna	0.315	0.552
saligna – stolonifera	0.356	0.556
lindleyi – pruinescens	0.445	0.647

Overall, native models trained using all *A. saligna* records, or records per subspecies, displayed perfect sensitivity but variable modelled prevalence (Table 2, Fig. S1, S4; aim 1). Models for pairwise comparisons between the subspecies displayed the highest levels of sensitivity and modelled prevalence for models trained with subspecies *lindleyi* and *pruinescens*, while pairwise comparisons for models trained with subspecies *saligna* and *stolonifera* produced much lower sensitivity and modelled prevalence (Table 2).

Models projected to South Africa

All models projecting to the introduced range in South Africa displayed statistically significant results according to the exact binomial test ($P < 0.0001$, Table 2). Within full native model projections (MESS+ and MESS− areas; Fig. 3b–j), no single model was able to predict the full current distribution of *A. saligna* in South Africa (i.e. no model obtained perfect sensitivity; Table 2, aim 2). Sensitivity was highest for the models trained using South African records (0.99, Table 2) and displayed almost no MESS− regions (Fig. 3a, S2, S4). Sensitivity of models trained using native records was highest for the pairwise model for subspecies *lindleyi* and *stolonifera* and the individual model for subspecies *lindleyi* (Table 2). All these models displayed low modelled prevalence (Table 2). The largest areas of modelled prevalence (Table S2) were for subspecies *saligna* (Fig. 3e) and *pruinescens* (Fig. 3d); however, much of this area fell within MESS− areas (model extrapolation, Fig. S2).

Models trained with native records and projected to South Africa indicate that the Western and Northern Cape had climates similar to those used to construct the model in the native range in Australia (i.e. MESS+ areas Fig. 3b–j) and were not limited by any single bioclimatic variable (Fig. S3). Within these MESS+ areas and across all native models, regions that were projected to be climatically suitable were consistent with at least some of the current introduced distribution of *A. saligna* (Fig. 3b–j, Table 2, aim 2).

Table 2 Correlative model fit based on the sensitivity and modelled prevalence of distribution models developed for *Acacia saligna* relative to each of the three aims. The training and testing data sets and the region of projection varied between models and were grouped based on the aims.

Aim	Subspecies training data	Testing data set	Region of projection	Sensitivity	Modelled prevalence
(1) Assess whether the subspecies occupy areas in their native range that can be distinguished by correlative models	All subspecies	All subspecies	Western Australia	1.00	0.53
	A.s. ssp. *lindleyi*	*A.s.* ssp. *lindleyi*	Western Australia	1.00	0.54
	A.s. ssp. *pruinescens*	*A.s.* ssp. *pruinescens*	Western Australia	1.00	0.34
	A.s. ssp. *saligna*	*A.s.* ssp. *saligna*	Western Australia	1.00	0.17
	A.s. ssp. *stolonifera*	*A.s.* ssp. *stolonifera*	Western Australia	1.00	0.09
	A.s. ssp. *lindleyi*	*A.s.* ssp. *saligna*	Western Australia	1.00	0.55
	A.s. ssp. *lindleyi*	*A.s.* ssp. *pruinescens*	Western Australia	0.98	0.55
	A.s. ssp. *lindleyi*	*A.s.* ssp. *stolonifera*	Western Australia	1.00	0.55
	A.s. ssp. *pruinescens*	*A.s.* ssp. *lindleyi*	Western Australia	0.76	0.35
	A.s. ssp. *pruinescens*	*A.s.* ssp. *saligna*	Western Australia	1.00	0.36
	A.s. ssp. *pruinescens*	*A.s.* ssp. *stolonifera*	Western Australia	1.00	0.36
	A.s. ssp. *saligna*	*A.s.* ssp. *lindleyi*	Western Australia	0.37	0.15
	A.s. ssp. *saligna*	*A.s.* ssp. *pruinescens*	Western Australia	0.24*	0.15
	A.s. ssp. *saligna*	*A.s.* ssp. *stolonifera*	Western Australia	0.61	0.15
	A.s. ssp. *stolonifera*	*A.s.* ssp. *lindleyi*	Western Australia	0.09*	0.07
	A.s. ssp. *stolonifera*	*A.s.* ssp. *pruinescens*	Western Australia	0.71	0.07
	A.s. ssp. *stolonifera*	*A.s.* ssp. *saligna*	Western Australia	0.52	0.07
(2) Explore predictive power of models in South Africa relative to current molecular information	All subspecies	South African *A. saligna*	South Africa	0.73	0.03
	A.s. ssp. *lindleyi*	South African *A. saligna*	South Africa	0.90	0.04
	A.s. ssp. *pruinescens*	South African *A. saligna*	South Africa	0.41	0.18
	A.s. ssp. *saligna*	South African *A. saligna*	South Africa	0.29	0.49
	A.s. ssp. *stolonifera*	South African *A. saligna*	South Africa	0.17	0.00
	pruinescens+saligna+stolonifera	South African *A. saligna*	South Africa	0.44	0.02
	lindleyi+pruinescens+saligna	South African *A. saligna*	South Africa	0.69	0.03
	stolonifera+lindleyi	South African *A. saligna*	South Africa	0.91	0.04
	pruinescens+saligna	South African *A. saligna*	South Africa	0.41	0.01
	South African *A. saligna*	South African *A. saligna*	South Africa	0.99	0.12
	South African *A. saligna*	All native subspecies	Australia	1.00	0.23
(3) Predict which subspecies are present in other countries	All subspecies	Mediterranean *A. saligna*	Mediterranean Basin	0.61	0.24
	A.s. ssp. *lindleyi*	Mediterranean *A. saligna*	Mediterranean Basin	0.22*	0.29
	A.s. ssp. *pruinescens*	Mediterranean *A. saligna*	Mediterranean Basin	0.04	0.42
	A.s. ssp. *saligna*	Mediterranean *A. saligna*	Mediterranean Basin	0.04*	0.02
	A.s. ssp. *stolonifera*	Mediterranean *A. saligna*	Mediterranean Basin	0.00*	0.00
	South African *A. saligna*	Mediterranean *A. saligna*	Mediterranean Basin	0.30*	0.19

*Statistically non-significant results based on the exact binomial test ($P > 0.05$).

Note: Model sensitivity was defined as the proportion of correctly predicted observed presences, where presence was defined by the lowest presence threshold (LPT) at which there was an actual presence in the projected range. Modelled prevalence was defined as the proportion of complete projection region estimated to be climatically suitable.

Within MESS− areas, models varied in their ability to correctly predict areas of climatic suitability within the distribution of *A. saligna*. Models that were built on combinations of subspecies occurrences did not project climatically suitable areas in the northern parts of South Africa in areas far beyond the known distribution of *A. saligna* (Fig. 3g–j). However, individual models for subspecies *saligna* (Fig. 3d) and *pruinescens* (Fig. 3d) projected climatic suitability along the east coast of South Africa, consistent with known occurrences of *A. saligna*. For these models, the dominant climatic variable (limiting factors, *sensu* Elith *et al.*, 2010) influencing model projections in the north-eastern regions of South Africa was precipitation in the hottest quarter (Bio18, Fig. S2b,c). In these cases, Bio18 displayed open-ended response curves that maintained high suitability values (Fig. S2b,c).

South African models projected to Australia

Models constructed using introduced South African records and back projected to Australia displayed statistically significant results according to the exact binomial test ($P < 0.0001$, Table 2, aim 2). Regions of high projected suitability occur along the coastal regions of south-western Western Australia,

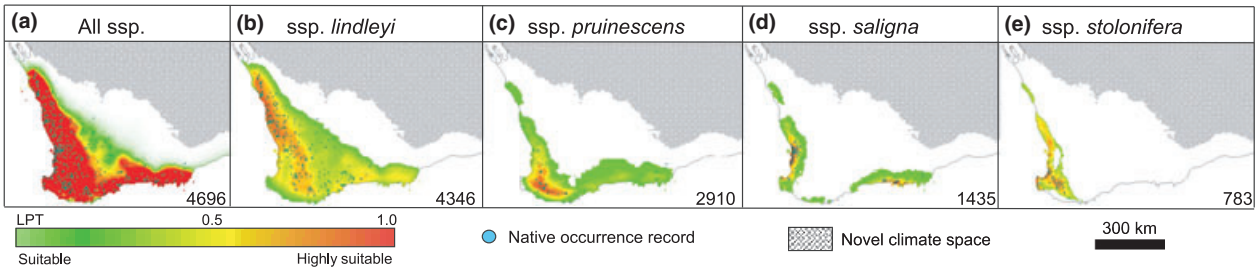

Figure 2 Projected bioclimatic niches identified by correlative distribution models for each subspecies of *Acacia saligna* in Western Australia. Projections were based on the mean of 10 replicate models. The colour scale depicts areas of projected climatic suitability, (≥ lowest presence threshold, LPT), ranging from highly suitable (red) to suitable (yellow) to marginally suitable (green) and unsuitable (white). Models were calibrated with native occurrence records from Western Australia (blue circles) and pseudo-absence data drawn from a single, environmentally informative background. The number of 5-min grid cells projected as climatically suitable by each model, i.e. the size of the projected range, is shown in the bottom right corner. Hatched overlays indicate areas of model extrapolation (MESS−; i.e. at least one climatic variable has a value outside the range of the variables in the training region).

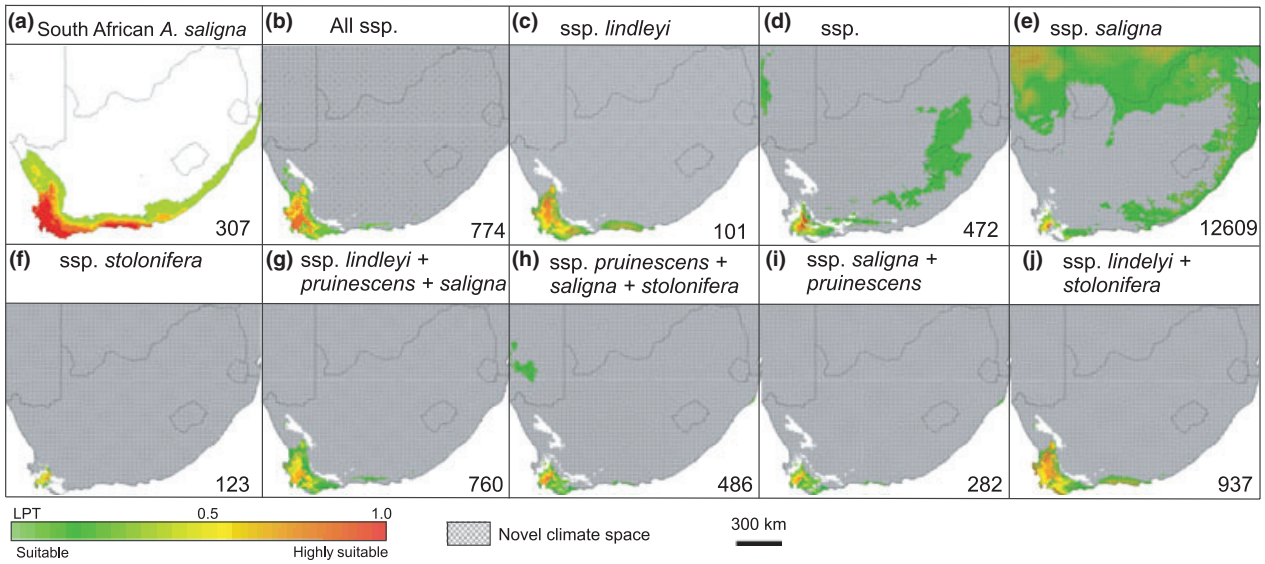

Figure 3 Variation in the bioclimatic niches identified by correlative distribution models in the introduced range of *Acacia saligna* in South Africa. Potential distributions were constructed considering current molecular data from Le Roux *et al.* (2011) and aimed to predict which subspecies are likely to be present in South Africa. Projections were based on the mean of 10 replicate models and were calibrated with (a) introduced South African occurrences, (b) all native occurrences, (c–f) native occurrences per subspecies and (g–j) various combinations of subspecies. Pseudo-absence data were drawn from a single, environmentally informative background. The colour scale depicts areas of projected climatic suitability, (≥ lowest presence threshold, LPT), ranging from highly suitable (red) to suitable (yellow) to marginally suitable (green) and unsuitable (white). The number of 5-min grid cells projected as climatically suitable by each model, i.e. the size of the potential introduced range, is shown in the bottom right corner. Hatched overlays indicate areas of model extrapolation (MESS−; i.e. at least one climatic variable has a value outside the range of the variables in the training region).

consistent with the native distribution of *A. saligna* (Fig. 4, blue circles). These models suggest that the entities present in South Africa occupy at least the full native niche of *A. saligna*, i.e. perfect sensitivity (Table 2). Moreover, projected climatic suitability extended in a north-easterly direction beyond the native range of *A. saligna* into the inland areas of south-western Western Australia (Fig. 4). However, areas of projected suitability did not include the full introduced range of *A. saligna* in eastern Australia (Fig. 4, black circles), despite projected suitability intersecting with the majority of naturalized occurrences of *A. saligna* in this region. Taken together, these models suggest that there may be additional regions of climatic suitability for (South African) *A. saligna* in south-western Western Australia and eastern Australia (MESS+ space) that are not currently occupied.

Models projected to the Mediterranean Basin

Only models for all subspecies combined, and subspecies *pruinescens* projecting to the introduced range in the

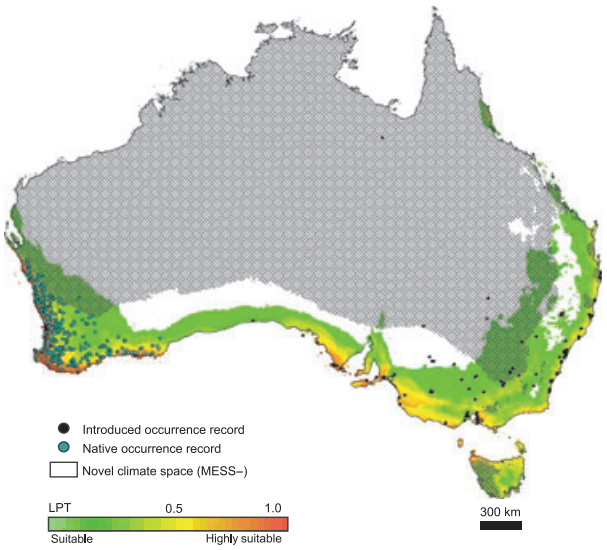

Figure 4 Projected bioclimatic niches of introduced South African populations of *Acacia saligna* in Australia. Projections were based on the mean of 10 replicate models and aimed to assess niche differences between the Western Australian niche and the South African niche within the same bioclimatic space. South African pseudo-absence data were drawn from a single, environmentally informative background. The colour scale depicts areas of projected climatic suitability, (≥ lowest presence threshold, LPT), ranging from highly suitable (red) to suitable (yellow) to marginally suitable (green) and unsuitable (white). Hatched overlays indicate areas of model extrapolation (MESS−; i.e. at least one climatic variable has a value outside the range of the variables in the training region).

Mediterranean Basin displayed statistically significant results according to the exact binomial test ($P < 0.0001$, Table 2, aim 3). Areas of projected climatic suitability in the Mediterranean Basin (Fig. 5) and modelled prevalence and sensitivity (Table 2, aim 3) varied substantially between subspecies. Models displayed the highest sensitivity for projections trained using all native records, followed by models trained with South African records, followed by models trained with subspecific records (Table 2). Overall, a large proportion of the Mediterranean Basin represented MESS− climates relative to the native range of *A. saligna* (Fig. 5a,c–f). Models trained using introduced South African records produced the smallest MESS− area (Fig. 5b). Within MESS− and MESS+ space, no model projected climatic suitability intersecting with all known occurrences in the region (i.e. perfect sensitivity was not achieved).

DISCUSSION

Our models indicate that all subspecies of *A. saligna* occupy different climatic niches within their native ranges. This variation in climatic space is confirmed by multiple lines of evidence: model projections, quantification of climate occupancy, and the sensitivity and modelled prevalence of projections. The degree of dissimilarity between model projections for the four subspecies and their combination projections (i.e. models calibrated with groups of subspecies) to South Africa indicate that the realized niches will likely differ irrespective of the morphological (Maslin *et al.*, 2006) or genetic groupings (Millar *et al.*, 2011).

Our models show that in Western Australia *A. saligna* subspecies *stolonifera* occupies the most spatially and climatically narrow niche, while *A. saligna* subspecies *lindleyi* occupies the widest niche. Assuming that subspecies distributions are primarily defined by climatic limitations, this suggests that subspecies *lindleyi* followed closely by subspecies *pruinescens* have the widest environmental tolerance. These subspecies should be considered a slightly higher risk of becoming naturalized elsewhere, relative to the other subspecies.

Models projecting to the introduced range of *A. saligna* in South Africa indicate that South African populations currently occur outside the range of climates occupied by all native subspecies, as represented by the climatic variables used in our modelling. Moreover, models for *A. saligna* subspecies *lindleyi* and the combination model of subspecies *lindleyi* + *stolonifera* most closely reflect *A. saligna*'s current introduced distribution in South Africa. Phylogeographic data from Western Australian and South African *A. saligna* populations suggest a substantial genetic bottleneck and the presence of only a subset of the native subspecies in South Africa (Le Roux *et al.*, 2011). Based on the assumption that the native geographical distribution of these subspecies is partially explained by the climatic variables used to build the models in this study, it is most likely that either subspecies *lindleyi* or *stolonifera* are present in South Africa. However, back projections to Australia are inconsistent with native projections to South Africa, as they suggest that the South African entities occupy a wider climatic space than the currently occupied native range of *A. saligna*. That is, the drier inland regions of Western Australia and eastern Australia would be occupied by South African entities.

Models projecting to the Mediterranean Basin do not provide evidence linking a particular *A. saligna* subspecies to the introduced range as no model intersected with all known occurrences in the region. However, projections for subspecies *pruinescens* intersected with known occurrences of *A. saligna*, but these were within novel climate space. This suggests these subspecies would be most suited to the climates in the Mediterranean Basin. We caution that it would be imprudent to interpret these results as meaning that the other subspecies pose a lower risk of becoming invasive in areas with mediterranean-type climates.

In the light of these findings, it is important to consider the influence that a species' introduction history can have on the genetic structure in the introduced range (see Le Roux *et al.*, 2011). *Acacia saligna* was introduced on a number of occasions and has been widely and actively distributed in South Africa (Shaughnessy, 1980; Poynton, 2009). Despite the multiple introductions, our modelling suggests that not all native genetic entities are present in South Africa. This is in agreement with the amount of genetic diversity found in Australia, compared with South Africa (Le Roux *et al.*, 2011).

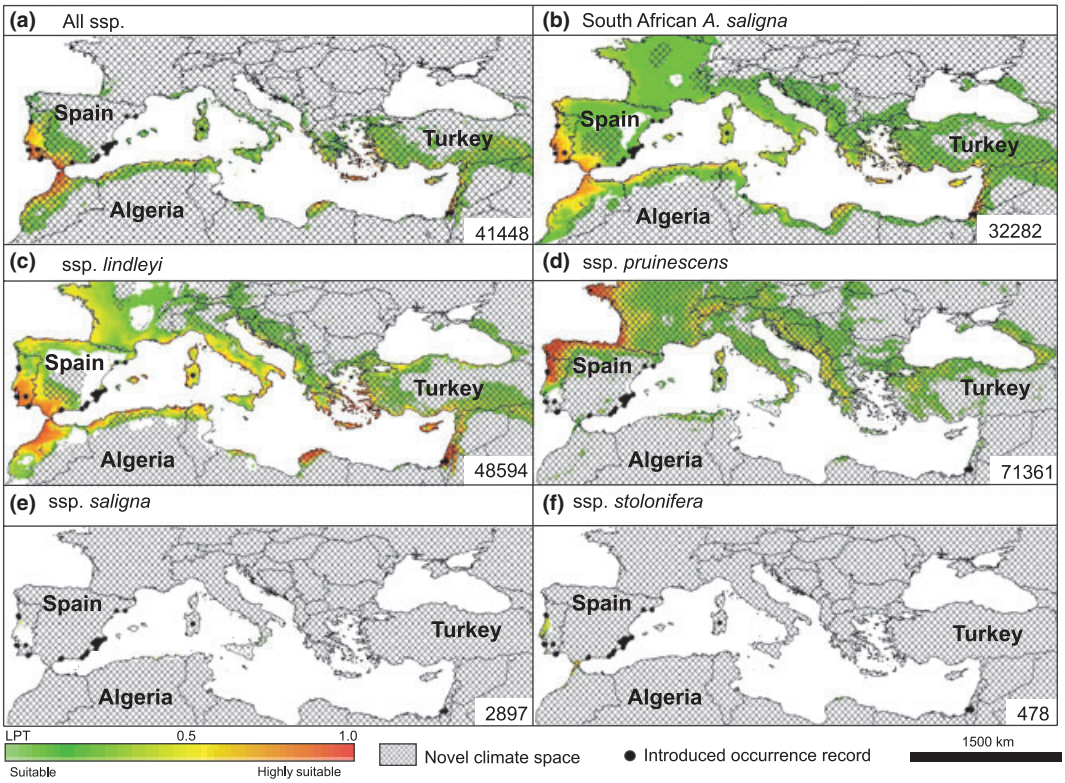

Figure 5 Projected bioclimatic niches of *Acacia saligna* in the Mediterranean Basin. Projections were based on the mean of 10 replicate models and aimed to predict which subspecies are likely to be present in a biogeographical region similar to the native range in Western Australia and the introduced range in South Africa. Models were calibrated with (a) all native occurrences; (b) introduced South African occurrences; and (c–f) native occurrences per subspecies. Pseudo-absence data were drawn from a single, environmentally informative background. Hatched overlays indicate areas of model extrapolation (MESS−; i.e. at least one climatic variable has a value outside the range of the variables in the training region). The colour scale depicts areas of projected climatic suitability (≥ lowest presence threshold, LPT) ranging from highly suitable (red) to suitable (yellow) to marginally suitable (green) and unsuitable (white). The number of 5-min grid cells projected as climatically suitable by each model, i.e. the size of the projected range, is shown in the bottom right corner. Hatched overlays indicate areas of model extrapolation (MESS−; i.e. at least one climatic variable has a value outside the range of the variables in the training region).

In addition, our models were unable to confirm the presence of only one particular subspecies or genetic group in South Africa. It may also be that a niche shift has taken place; this would explain the inability of all models built with native data to predict the introduced distribution in South Africa. A shift may also be due to novel genetic entities that have arisen in the invasive range or the impact of human mediated dispersal (e.g. Theoharides & Dukes, 2007). These uncertainties highlight the need for further research on the link between genetic variation and niche partitioning in the native and introduced range of invasive species, and the use of common garden experiments to elucidate links between genetic variation and quantifiable differences in plant fitness.

In summary, although the models displayed high levels of subspecific predictability (i.e. high sensitivity and relatively low prevalence) in their native range, they displayed poor predictability when applied to their introduced ranges. This may be due to a niche shift upon introduction (e.g. genetic drift) or that the SDMs developed for *A. saligna* do not incorporate climatic variables that are restricting the species' current distribution. The very gradual climatic gradients in the south-west of Western Australia mean that the absolute differences in climate space between the subspecies may be far smaller relative to the range experienced in other mediterranean-type regions to which the species has been introduced and that factors other than climate may also be important for explaining range limits in Australia. We recognize, for example, that non-climatic variables such as edaphic features may also influence the niche occupied by *A. saligna*. However, we were unable to account for such influences owing to a lack of appropriate data for all the regions we investigated.

This study represents the first SDM to be developed for an invasive plant species complex. Models showed that subspecies of *A. saligna* vary substantially in their climatic and spatial extent in Western Australia, providing evidence that SDMs can detect bioclimatic niche differences below the species level. Further, we found that models based on data from the native range did not adequately predict the distribution of *A. saligna* in South Africa or the Mediterranean Basin. These

findings provide putative support for the observations that genetic diversity and structure in the South African range differ considerably from the native range and are consistent with the molecular data of Le Roux *et al.* (2011). Furthermore, we provide evidence for a lack of niche conservatism between the native and introduced range of *A. saligna*. Further research is required to test whether niche conservatism is violated between the native and introduced range of other species.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1 Bioclimatic response curves for the variables used to construct native projections.

Figure S2 Bioclimatic response curves for the variables used to construct South African projections.

Figure S3 Limiting bioclimatic variables for native and introduced projections.

Figure S4 Variable contributions, training and testing gains for native and introduced projections.

Table S1 Multicollinearity of the bioclimatic variables used to construct models.

Table S2 Data sets and projection regions used to conduct modelled prevalence and sensitivity values.

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BIOSKETCH

This research is part of a project using genetic techniques to improve our understanding and management of invasive alien plant species in South Africa at the Centre for Invasion Biology (CIB; http://www.sun.ac.za/cib). **Genevieve Thompson** is currently undertaking her PhD at the CIB, with a research focus on the population genetics, biogeography and environmental distribution of invasive acacias.

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